Form and Function of the Radulae of Pleurotomariid Gastropods

by

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Abstract. Detailed examination of the radulae of *Pleurotomaria (Perotrochus) midas* Bayer, 1965, and *P. (P.) quoyana* Fischer & Bernardi, 1856, leads to new conclusions regarding the form and function of the radula of the most primitive extant marine gastropods. A number of morphological features are interpreted as mechanical adaptations for dealing with stress and efficient accommodation of teeth when the radula is not in use. The terminal structures of the characteristic pleurotomariid "bristle tooth" are found to lack the flexural stiffness that has been attributed to them. They are highly flexible and may lie in tangled disarray after use in feeding. Independent evolution of similar teeth in *Seila* A. Adams, 1861, an unrelated mesogastropod that also feeds upon sponges, suggests that the morphology is not ancient or phylogenetically constrained so much as it is functionally constrained. Independent lines of evidence suggest that the radulae of living pleurotomariids offer few clues as to the radular morphology of ancient marine gastropods and the primitive state of the molluscan radula.

INTRODUCTION

IT IS A matter of longstanding record that the living species of pleurotomariid gastropods share a peculiar radular morphology. Descriptions and line drawings (DALL, 1889; BOUVIER & FISCHER, 1899; WOODWARD, 1901; BARNARD, 1963; AZUMA, 1964; FRETTER, 1964, 1966; HYMAN, 1967; BOUCHET & MÉTIVIER, 1982) have emphasized the numbers of different kinds of teeth and, especially, the presence of numerous plates terminating in "brushes," "tufts," or "bristles." The details of form and the inferred function of these teeth have not been considered closely, and the terms "brush" and "bristle" may be inappropriate and misleading in terms of functional and mechanical properties.

Use of the term "hystricoglossate" (HYMAN, 1976:236) to describe the pleurotomariid radula emphasizes the distinctness from more typical rhipidoglossate archaeogastropod radulae and reinforces the notion that the terminal structures of the unique teeth are mechanically stiff or of very limited flexibility. Data from gut contents and observations of the substrata from which specimens have been taken or observed alive suggest that the animals feed primarily by "grazing" on communities of encrusting invertebrates, predominantly sponges (WOODWARD, 1901; THIELE, 1935; YONGE, 1973; ROPER, personal communication, 1975; HICKMAN, 1976; ARAKAWA *et al.*, 1978). The bristle teeth have, therefore, been implicated as adaptations for sponge feeding, and WOODWARD (1901) pro-posed that the bristles might be used to remove "flesh" from sponge spicules.

Examination of the radulae of two species over a range of magnifications with conventional light microscopy and scanning electron microscopy reveals a number of new features and permits reevaluation of the pleurotomariid radula. The primary objectives of this paper are to describe and illustrate the dentition, to reconsider the function of the "bristle teeth," and to consider the evolution of this peculiar morphology in relationship to a close convergence with structures in the radula of a sponge-feeding cerithiopsid gastropod.

MATERIALS AND METHODS

Radulae were removed from preserved specimens by middorsal incision of the buccal cavity after observation of the configuration of the radular ribbon and its relationship to the odontophore. Radulae were cleaned in distilled water after brief immersion in 10% sodium hydroxide to macerate and remove extraneous proteinaceous material. Manipulation of the radulae under low power of a light microscope was used to establish topographic relationships and the range of obvious and easily facilitated mechanical movements of major fields of radular teeth. Radulae were then divided into a series of segments, placed in vials numbered from anterior to posterior, and run through a graded alcohol series from 70 to 100% to remove as much water

as possible prior to drying for scanning electron micros-copy.

Some segments were set aside for further examination with light microscopy. The anteriormost segment and seg-ments from the fully formed but unused mid portion of the radula of each species were further cleaned in an ul-trasonic cleaner and air dried. In addition, individual teeth and clusters of teeth of different morphologies were cleaned and air dried. Dried radular material was attached to SEM stubs, coated with gold, and examined at low ac-celerating voltages following procedures outlined by HICKMAN (1981, 1983). Similar preparations were made of radulae of related pleurotomariacean gastropods in the families Scissurellidae and Haliotidae and of a sponge-feeding cerithiopsid mesogastropod of greater phylogenet-ic distance but similar feeding ecology.

RESULTS

Central Tooth Field

The major features of the pleurotomariid central tooth field are illustrated in Figure 1. Figures 2 and 3 provide comparable illustrations of the central tooth fields of the other two families in the Pleurotomariacea, the Scissurel-lidae and the Haliotidae. The major characteristics of the pleurotomariid radula are as follows: (1) The teeth in the central field are obscured in the flat-lying excised radula by the larger and more well-developed marginal tooth fields. (2) The teeth in a half row of the central field are arranged with both cusps and bases in a characteristic "V" shape. (3) The number of teeth in the central field (as many as 59) is greater than in any known proso-branch. (4) The central field is asymmetric, and there are a number of distinctive features of the asymmetry: the rachidian tooth is, itself, asymmetric (Figure 4); the teeth within the central complex on either side of the rachidian

have their bases and cusps positioned asymmetrically rel-ative to the mirror plane perpendicular to the plane of the radular ribbon; and the skewing of the asymmetry may be either to the left or the right. It is, for example, right-skewed in *Pleurotomaria (Perotrochus) quoyana* and left-skewed in *Pleurotomaria (Perotrochus) midas* (Figures 4 and 5, respectively). This form of asymmetry has evolved independently in a number of prosobranch lineages, as pointed out previously by HICKMAN (1982; 1984). (5) There are three major types of teeth in the central field: the asymmetric rachidian, hooded and irregularly formed inner laterals, and a set of more regularly developed outer laterals that grade from a simple lamellar form to com-plexly reinforced and cusped. These tooth types are de-scribed more fully below.

Rachidian: The rachidian is a narrowly elongate struc-ture that may be irregular in its development, its folded appearance, and the sometimes ragged terminal end. It generally has thin lateral folds that overlap similar lateral folds on the two inner lateral teeth. Although the rachid-ian tapers distally and may be folded into an acutely pointed terminus, one would not call it a standard cusp, nor is an obvious function suggested.

Inner laterals: The first three or four teeth on either side of the rachidian are similar to the rachidian in their broad, thin, and folded form. The inner pair is the largest, and each has an irregularly enlarged hood-like distal termi-nation that faces away from the rachidian and partially enfolds and covers the terminations of the adjacent and smaller inner lateral teeth. The remaining inner laterals are progressively smaller and with less well-developed hood-like terminations.

Outer laterals: The outer lateral teeth, which have been referred to as "lamellate" by some authors (BARNARD, 1963; FRETTER, 1964, 1966; HYMAN, 1967:237), are com-

Explanation of Figures 1 to 9

Figure 1. *Pleurotomaria (Perotrochus) quoyana* Fischer & Ber-nardi, 1856. Rachidian and lateral teeth. University of Miami, Rosenstiel Institute of Marine Science, Gerda Sta. G-897. Bar = 200 μm.

Figure 2. *Haliotis rufescens* Swainson, 1822. Rachidian, lateral, and inner marginal teeth. University of California, Museum of Paleontology Loc. UCMP R-3200. Bar = 200 μm.

Figure 3. *Scissurella crispata* (Fleming, 1828). Rachidian, lateral, and inner marginal teeth. R/V *Oregon* Sta. BMT-9. Bar = 40 μm.

Figure 4. *Pleurotomaria (P.) quoyana.* Asymmetric rachidian and skewed lateral tooth rows with right laterals situated farther anterior than corresponding left laterals. Specimen same as Fig-ure 1. Bar = 200 μm.

Figure 5. *Pleurotomaria (P.) midas* Bayer, 1965. Asymmetric rachidian and skewed lateral tooth rows with left laterals situ-

ated farther anterior than corresponding right laterals. Univer-sity of Miami, Rosenstiel Institute of Marine Science, Gerda Sta. G-10-16. Bar = 500 μm. Figures 6 to 9 are from the same radula.

Figure 6. Right outer lateral teeth in the region of transition from lamellar plates (on left) to larger teeth with terminal and subterminal denticles (on right). Bar = 400 μm.

Figure 7. Enlarged view of left outer lateral teeth oriented to show ridges or thickenings on compressional surfaces of cusps. Bar = 200 μm.

Figure 8. Transition from lateral to marginal teeth. Right outer lateral teeth are above and right inner marginals (sickle teeth) are below. Bar = 400 μm.

Figure 9. Transition from inner to outer marginals. Right inner marginal sickle teeth are above and right outer marginal fila-ment-tipped teeth are below. Bar = 400 μm.
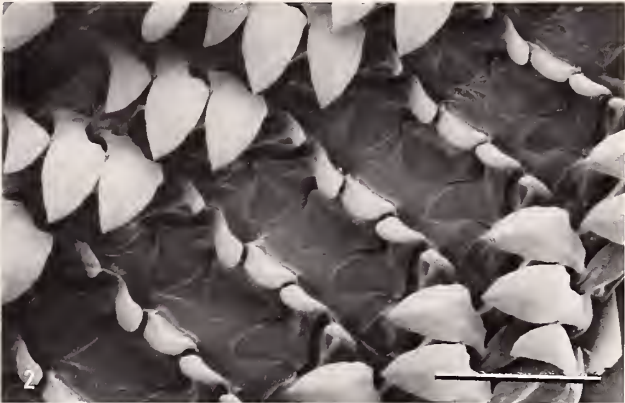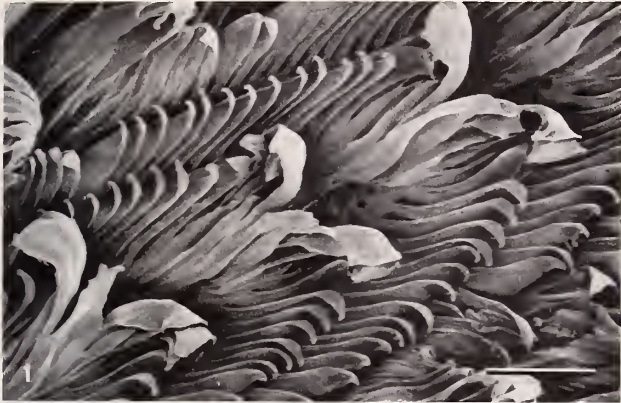
plex both in their row configuration and in the morphological gradation within rows. They are numerous (24–26 per half row), and they are arrayed with their bases and cusps forming a "V." The first 18 to 20 teeth on the inner segment of the "V" are relatively thin lamellar plates, each with a small terminal bend or fold that might be called a cusp. The plates are thickened on their inner margins by enrolling of the edge. At the base, the partially enrolled edge is expanded and attached to the radular membrane in a configuration that should facilitate twisting of the plate and allow more freedom in its movement. The teeth along this segment of the "V" are aligned nearly parallel to the longitudinal axis of the radula rather than in more standard "transverse" rows. When the radula is viewed in cross section, these teeth lie in topographic "gullies," somewhat lower than the larger and more expanded rachidian and inner laterals, and much lower than the well-developed marginal complexes. At the base of the "V" the outermost laterals begin to increase in length. They are no longer thin, small lamelliform elements, but become complexly reinforced in cross-sectional shape and develop both a terminal and a subterminal pointed denticle. The transition in this region of the radula is illustrated in Figure 6. On the convex or compressional surface of the cusps, thickenings or "compressional ridges" (HICKMAN, 1981) are evident (Figure 7). The form of such teeth implies contact with the substratum during feeding.

Marginal Tooth Fields

The major features of the pleurotomariid marginal tooth fields are several. (1) The most massive and most morphologically complex teeth are found in this portion of the radula rather than in the central tooth field. (2) The cross-sectional shape of the radula and its configuration in the animal relative to the odontophore suggest that the marginal teeth, rather than the central complex, are the major food-preparing structures. (3) The large inner marginal teeth are accommodated in the folded radula in alternating, zipper-like fashion from one side of a row to another.

(4) Three major types of teeth occur in each of the marginal fields: hook-shaped sickle teeth, the filament-tipped tangle teeth, and the paddle-shaped teeth. Each of these types is described below.

Sickle teeth: The innermost marginal teeth are the most formidable teeth in the pleurotomariid radula. Between 11 and 21 of these teeth occur in each half row. Other authors have referred to them as "hooked" teeth (FRETTER, 1964, 1966) or "falcate plates" (BARNARD, 1963; AZUMA, 1964). The abrupt transition from outer laterals to these teeth is illustrated in Figure 8. Although the term "hooked" does accurately portray the fact that the teeth are curved, it does not convey any notion of complex cross-sectional shape. The term "sickle" is a better descriptor not only of curvature, but also of the cross-sectional shape and the distribution of materials. The terminology is not intended to imply close similarity of function, however.

Filament-tipped teeth: The major portion of the marginal tooth complexes consists of so-called brush teeth (FRETTER, 1964, 1966), bristle teeth (HYMAN, 1967), or marginals with "tufts of bristles" (BARNARD, 1963). They have been considered to be unique to the pleurotomariid radula, and they are of a complex form that cannot be described fully using light microscopy and low magnification. There is also a heretofore undocumented discrepancy between the appearance of the morphology before and after use by the animal in feeding. The transition from sickle teeth to filament-tipped teeth is illustrated in Figure 9.

A typical unused but fully formed tooth from the middle of a half row has two types of terminal structures (Figure 10): a group of numerous, thin filaments that lie parallel to one another and, below them, a laterally flattened portion that is deeply notched to form three prominent blunt denticles. The innermost teeth within any half row tend to be more weakly denticulate and lack the filaments, while the outermost teeth lack denticles and the filaments are greatly shortened and reduced in number. The terminal end of a typical tooth is enlarged in Figure 10 to show both types of structure. Figure 11 provides a proximal

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Explanation of Figures 10 to 17

Figure 10. *Pleurotomaria (Perotrochus) midas* Bayer, 1965. Enlarged tip of a filament-tipped tooth showing filaments and subterminal denticles. Bar = 40 μm. This figure and Figures 11 to 15 are from the same radula illustrated in Figures 5 to 9.

Figure 11. Filament-tipped tooth showing region in which filaments arise from tooth shaft in parallel series. Bar = 20 μm.

Figure 12. Detail of the distal end of two filament clusters to show branching of individual filaments. Bar = 10 μm.

Figure 13. Shafts and terminal filaments viewed from above to show flattening of tooth shafts. Concave surfaces on left face central axis of radula. Bar = 100 μm.

Figure 14. Region of origination of filament clusters viewed from above to show two series arising one on either side of a central subcylindrical pit. Bar = 20 μm.

Figure 15. Used filament-tipped teeth from the anterior end of the radula. Bar = 100 μm.

Figure 16. *Pleurotomaria (P.) quoyana* Fischer & Bernardi, 1856. Used and worn teeth from anterior end of radula. Bar = 400 μm.

Figure 17. *Seila terebelloides* (Hutton, 1873). Marginal teeth showing convergent development of terminal filaments and subterminal denticles. University of California, Museum of Paleontology Loc. UCMP D-9044. Bar = 4 μm.
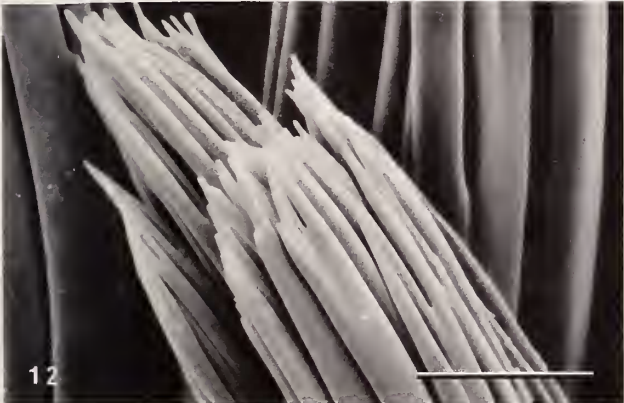
detail of the pattern by which filaments arise in parallel series from the flattened tooth shaft, while Figure 12 is a detail of the distal end of two filament clusters, showing that each filament may branch four or five times to form a secondary cluster of terminally pointed filaments.

The entire shaft of the tooth is flattened and slightly concavo-convex, as illustrated by viewing the teeth from above (Figure 13). The concave surface is the surface nearest the central axis of the radula, and it is the leading edge in sweeping movements of the teeth. When the region of origination of the filaments is viewed at even higher magnification from above (Figure 14), two parallel series of filaments and a central subcylindrical pit are evident.

Nothing in the appearance of these unworn teeth contravenes the traditional notion of bristliness or mechanical stiffness. However, when they are manipulated while wet, it is clear that they lack flexural stiffness, and examination of teeth from the worn anterior end of the radula of *Pleurotomaria* (*Perotrochus*) *midas* shows the filaments in a tangled disarray that suggests more similarity to a mop than to a broom (Figure 15). However, this particular animal may, shortly before capture, have been radulating a substrate that produced an unusual wear pattern. This pattern has not been reported previously, and teeth from the same region of the radula of a specimen of *P.* (*P.*) *quoyana,* although showing evidence of flexibility and wear (Figure 16), are not in the same tangled state.

Paddle-shaped teeth: The final 6 to 10 teeth in each half row of the marginal complex are lacking in both filaments and terminal denticulation. They are flattened and bluntly paddle shaped. Flattened paddle-shaped teeth also occur singly as outermost marginals in some gastropods in the family Trochidae (HICKMAN, 1981), the prosobranch family that appears to be most closely related to pleurotomariids in a number of aspects of morphology and anatomy. The question of whether similarity of form is to be interpreted as indicative of phylogenetic affinity or as convergence related to function will be treated below.

The Radula of *Seila*

The filament-tipped teeth of *Pleurotomaria* have been considered unique among the Gastropoda. Although BARNARD (1963) followed other authors in considering this type of tooth to be characteristically pleurotomariid, he noted a similar morphology portrayed in THIELE's (1929) illustration of the radula of the cerithiopsid genus *Seila* A. Adams, 1861. Drawings in a recent monographic treatment (MARSHALL, 1978) further reinforce the similarity, and a scanning electron micrograph of the analogous tooth from the radula of *Seila terebelloides* (Hutton, 1873) is provided for comparison in Figure 17.

DISCUSSION

Although pleurotomariid gastropods attract considerable attention as collector's items, as objects of great beauty,

and as "living fossils," the foregoing detailed description and illustration are not provided simply to add to the mistique already surrounding these animals. Previously unappreciated morphological features of the radulae of living pleurotomariids provide a basis for reconsidering the function of the morphology and the extent to which morphology is a reflection of heritage from a Paleozoic ancestor that had a primitive gastropod radula.

How Primitive is the Pleurotomariid Radula?

In its anatomy and basic shell form, living *Pleurotomaria* displays many features of gastropod organization that are inferred to be primitive and that have been abandoned in the course of Phanerozoic gastropod evolution. However, neither the long evolutionary history of pleurotomariids nor the conservative evolution of the shell justify concluding that the radula is conservative. In fact, several reasons suggest that the radula is highly specialized and may bear little resemblance to the radulae of ancient Paleozoic pleurotomariaceans.

The first reason for caution is the dissimilarity between the radulae of large, living slit shells and those of scissurellids and haliotids, members of the other two extant pleurotomariacean families (Figures 1 to 3). The evolution of diverse radular morphology within the superfamily shows no shared elements to suggest a unified primitive superfamilial plan that has been resistant to change. The second reason for caution is the difference in ecology separating Paleozoic and Mesozoic pleurotomariaceans from living species (HICKMAN, 1976). The early fossil record of slit shells occurs predominantly in shallow-water deposits, where shells are found in association with reef-building and reef-inhabiting organisms. The living slit shells, on the other hand, are restricted to relatively deep water and rocky substrates. The encrusting invertebrates with which *Pleurotomaria* has been observed and the presence of abundant sponge spicules in the gut suggest an unusual form of "grazing" and source of nourishment. The large number of teeth per transverse row in the radula of *Pleurotomaria* is frequently cited as a primitive feature (HYMAN, 1967:236). It can be generalized that prosobranch evolution, as inferred from features other than the radula, is accompanied by progressive reduction in the numbers of teeth per row and the number of different kinds of teeth in the radula. It would be unwarranted to reject the possibility that *some* features of the *Pleurotomaria* radula are conservative; but it seems unlikely that, in morphological detail, we are glimpsing a feeding organ preserved from the Paleozoic era.

To What Extent Does Pleurotomariid Radular Morphology Reflect Function?

If radular morphology in the Pleurotomariidae has not been constrained closely by a plan that could not be changed readily, we can assume that some of the variation

and complex form has evolved either as mechanical alteration of the apparatus or as solutions to problems of preparing and ingesting particular kinds of food resources. It is tempting to conclude that many of the unusual features of the radula are adaptations for sponge feeding, but demonstrations of how an apparatus works and how efficiently it works go beyond the trivial observation that it does work.

Without knowing anything about the properties of the substrates on which the apparatus is used, little can be concluded about the suitability of design for preparing and gathering food. However, a number of features are subject to mechanical interpretation (*sensu* HICKMAN, 1981).

The topological arrangement and the irregular and underdeveloped morphology of elements in the central field both suggest that the central field acts mechanically to separate the marginal fields rather than to actively prepare and gather food. The asymmetry of the central field and its facilitation of alternatively interleaved accommodation of the rows of large sickle-shaped inner marginals further suggest a predominantly (not necessarily exclusively) non-feeding function for the central complex. Features such as compressional ridges on the outermost lateral teeth and the pattern of distribution of materials in the sickle-shaped teeth, as well as the concavo-convex cross-sectional shape of the shafts of the filament-tipped teeth, suggest mechanisms for dealing with different forms of stress. They are similar in form to engineering solutions to dealing with stress in man-made structures or implements.

Mechanical behavior of materials, such as the flexibility of filaments in the radular elements previously called "bristle" teeth, limits the possible range of functions. Finding these filaments in tangled disarray in the anteriormost portion of the radula demonstrates their flexibility and suggests that their function is not one requiring great flexural stiffness.

The bristle-like appearance of the distal end of the newly formed teeth provides a lesson in the analysis of morphology and the constraints on form (HICKMAN, 1981). The newly formed appearance of this particular morphology may not be providing us with information about phylogenetic or adaptive functional constraints so much as it is providing information about constructional constraints on how the building material can be secreted. Chitin can be secreted as separate fine filaments, but the filaments will be secreted in parallel rather than in the disarrayed configuration in which they are subsequently used.

Morphological Convergence in
Pleurotomaria and *Seila*

The strongest argument for a functional interpretation of the pleurotomariid filament-tipped teeth as adaptations to sponge feeding and the strongest argument against their interpretation as phylogenetically constrained conservative morphology is the appearance of remarkably similar teeth in the radula of sponge-feeding mesogastropods of the genus *Seila*. These observations do not confirm how the morphology is used, nor do they establish optimality of design; but the inference that selection has been operative is strong.

CONCLUSIONS

Interpretation of the unusual radular morphology of living pleurotomariid gastropods requires consideration of the alternative constraints of the long and conservative phylogenetic history of the superfamily, the mechanics of an apparatus that moves and deals with stress, the ecological factors involved in interaction of the apparatus with specific feeding substrates, the limitations of the material from which the apparatus is constructed, and the developmental limitations on how the material can be used to form individual teeth with fine morphological detail.

Several lines of evidence suggest that the radula of *Pleurotomaria* is not morphologically conservative or closely constrained phylogenetically and that it should not be taken as a representation of the primitive gastropod radula. The evolutionary results of mechanical constraints are visible primarily in the distribution of materials in individual teeth, particularly in cross-sectional shapes. Those teeth constructed to deal most effectively with stress are situated in the marginal tooth complexes rather than in the central complex, although it is in the innermost portions of the marginal complexes that most of the forces are apparently generated.

Demonstration of the flexibility of the elements formerly referred to as "bristles" requires an alternative interpretation of their mechanical function in feeding. Although sponge material has been reported as common in the gut contents of slit shells, it cannot be argued from morphology alone that the flexible filaments represent an adaptation for sponge feeding. The most powerful evidence that morphology is related to sponge feeding comes from the independent development of similar morphology in an unrelated group of sponge-feeding mesogastropods.

ACKNOWLEDGMENTS

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